A PRELIMINARY INQUIRY INTO THE SIGNIFICANCE OF TRACHEID-CALIBER IN CONIFERAE

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In connection with an investigation of the structure of the secondary wood of Indian species of *Pinus*, conducted by W. RUSHTON and myself (2), it seemed to me that some points of interest might be revealed by an inquiry into the relation between habitat and systematic affinity on the one hand, and, on the other, width of tracheid as measured in the spring zone. Fortunately, a comprehensive list of measurements of the diameters of such tracheids in American Coniferae is given by PENHALLOW (4). These, together with the measurements made by RUSHTON on Indian pines, serve as the basis for the succeeding discussion.

In framing conclusions regarding the significance of the statistics, there are a number of points of difficulty that can be removed only by further research or by information supplied by American botanists and foresters. And it is partly in the hope of exciting such research that this tentative inquiry is published. The difficulties are:

1. The caliber of the spring tracheids of a species varies in the same annual ring with height above the ground, and in different annual rings at the same level.

2. The caliber of the spring tracheids also varies in one and the same species according to the habitat in which the individual tree grows. A number of American species of *Pinus* and other conifers show considerable diversity in the habitat (edaphic and climatic) of the one and the same species.

Possibly one of the two causes above mentioned accounts for the discrepancy between PENHALLOW'S measurements and mine in connection with *Pinus glabra*.

3. Information as to the exact climate (rainfall and atmospheric humidity) of various habitats of species is lacking.

4. Information as to the exact edaphic conditions, and particularly as regards amount of moisture and level of the water-table,

are likewise wanting. To select one example. By several botanists *Pinus Jeffreyi* is described as growing on "dry" or "very dry" gravelly slopes. This statement aroused my doubt because the caliber of the tracheids, according to my hypothesis, seemed to speak in an opposite sense. On referring to H. MAYR's (3) work I found that he states that this gravel must contain a rich supply of water, though the water must not be stagnant.

5. Information as to depth of root is wanting. The lack of this information is especially significant in relation to American species of *Pinus*, which show so strong a tendency for growth on sandy soil. A species described as growing on dry sand may, by virtue of its long roots or a high water-table, be growing in wet sand.

6. Other features besides width of spring tracheid may affect the supply or expenditure of water, as thickness of sap wood, percentage of spring wood, size and structure of leaf, and aggregate surface (including duration) of the leaves of the species.

Despite the possibilities of disturbance by these factors, the evidence clearly points to the view that caliber of spring tracheids of different species varies directly with climatic or available edaphic humidity, and inversely as the conditions tending to induce desiccation. It also varies with the systematic position of the genus or species.

As I was working especially at the structure of the wood of *Pinus* and as this genus offers the largest number of species and the widest range of habitats of any American coniferous genus, the first inquiry concerns it.

Pinus

For the purpose of this discussion, the genus *Pinus* will be divided into two sections. Section I includes the species whose leaves are haploxylic, whose dwarf shoots have a more or less deciduous sheath, and whose wood has non-denticulate ray tracheids and bordered pits on the tangential walls of the outer summer tracheids. Section II includes diploxylic species with a persistent sheath, denticulate ray tracheids, and no universal tangential pitting in the outer summer tracheids. In the succeeding tables the mean diameter of the spring tracheid is the mean between the radial and tangential diameters.

Considering section I of *Pinus*, it is evident that the first six species, characterized by the narrowest spring tracheids, all occupy sites that are both edaphically dry and climatically dry for long

TABLE I

PINUS, SECTION I

	Mean diameter of spring tracheids in μ		Habitat*
	Atlantic	Pacific or North Mexican	
P. cembroides	....	24.0	Dry ridges, dry gravel, Arizona, Mexico, at 3500 ft.
P. edulis	....	24.5	Dry mesas, slopes, dry gravel, Colorado, Texas, New Mexico, up to 9000 ft.
P. Parryana	....	32.0	Arid mesas and desert slopes; subtropical in California and Lower California.
P. monophylla	....	33.0	Dry gravelly slopes, Utah to California, Arizona, at 3000–6000 ft.
P. Balfouriana	....	32.0	Often alpine, 5000–11,000 ft.; dry or rocky ridges and slopes in California.
P. aristata	....	33.5	Often alpine, up to 12,000 ft.; dry gravelly ridges in California, Nevada, Arizona, and Colorado.
P. albicaulis	....	35.0	Alpine; 53° N. to British Columbia to southern California, where it reaches 10,000 ft.
P. flexilis	....	39.0	Sandy-gravelly, sunny places, from British Columbia down to Texas, Arizona, S.E. California; attaining an altitude of 12,000 ft. in Montana; alpine also in Colorado.
P. reflexa	....	39.5	Cool moist ravines at 6000–8000 ft. in New Mexico and Arizona.
P. Strobus	41.5	....	Widespread in Canada and particularly the northeast of the United States; in the north on moist sandy or even swampy soil, but in the southern part of its area also on dry gravel.
P. monticola	....	43.0	British Columbia, southward to California, etc., 2000–10,000 ft.; in cultivation prefers airy, open, rather moist situations.
P. Lambertiana	....	45.0	Cascade and Coast Ranges in Oregon, southward along the coast to southern California, in rather moist soil with moist air.

*For particulars as to the habitats of the American Coniferae mentioned in this paper, I rely mainly upon the cited works of H. MAYR and C. S. SARGENT.

periods; two of them are also alpine species. The seventh species, *P. albicaulis*, also is alpine, but at least in the north is in a moister climate than are the preceding six, and there is no record that it is on a very pervious soil. The eighth, *P. flexilis*, is less alpine than

P. albicaulis. The ninth, *P. reflexa*, though in the climatically dry region, occupies moist sheltered spots. The remaining three species are in climatically moister regions, and one of them rather belongs to the Atlantic forest flora. The evidence, therefore, favors the view that narrowness of the spring tracheids is linked with special need for economizing water, and is thus encountered in xerophilous species.

But another interpretation is possible. The first six species, having the narrowest tracheids, all show wood of characteristic structure, differing from that of the others in that their ray parenchyma has "piceoid" pitting, and this conforms with characteristic cone structure, which agrees with that of diploxylic species. Thus these species belong to the peculiar subsection PARA-CEMBRA. Again, the first four of the species belong to one group of this subsection, namely PARRYA, while the remaining two belong to the other group BALFOURIA.

The remaining species differ from the first six in structure of medullary rays and of cone (whose scales have a terminal umbo), so that they are members of the subsection CEMBRA. And of them the first two species, with narrowest spring tracheids, belong to the subdivision of CEMBRA known as the group EU-CEMBRA; while the last four, with widest spring tracheids, are included in the other subdivision STROBUS.

Thus, in the whole series of species belonging to section I, diameter of spring tracheid is rigidly linked with systematic position. It is conceivable, therefore, on the one hand, that width of spring tracheid is a systematic or purely morphological character, not an epharmonic one; or, on the other hand, that these groups and subsections are not natural monophyletic groups, but are polyphyletic collections of types whose likenesses are determined by ecological factors. Yet, on the whole, it seems simplest to suppose that the evolution of section I of *Pinus* has been determined by available water supply, and that group PARRYA and group STROBUS represent extreme types, the former the most xerophilous and the latter the most hygrophilous.

The suggestions above given harmonize with the facts relating to East Indian pines. *P. Gerardiana*, belonging to the group PARRYA of the subsection PARA-CEMBRA, is xerophilous, has narrower spring tracheids than any other East Indian species, the width agrees sufficiently with those of American species, as it is 31.5 μ; that is, it would occupy, from the same point of view, a middle position if ranged among the American species of PARRYA. The other East Indian pine, *P. excelsa*, belonging to section I, is a member of the group STROBUS. Its habitat is not xerophilous, and its spring tracheids are 38.5 μ in diameter (compared with 41.5 μ of *P. Strobus*).

As table II shows, section II of *Pinus* displays no such simple systematic or ecological relations as does section I. This may be due partly to the difficulties mentioned before in appraising the habit and habitat of each species, and in part to defective classification of this large section.

The first three species in table II, having the narrowest spring tracheids (29.5–33 μ), are clearly xerophilous in habitat. One of the two Pacific types, *P. ponderosa* (29.5 μ), is, according to MAYR, the first pine encountered in going west from the prairies. A little farther west, while the narrower (moister) valleys include the moisture-loving Douglas fir and *P. monticola* (43 μ), the broader (drier) valleys are occupied by prairie or by *P. ponderosa*. Still farther west, on sandy soil, Douglas fir vanishes and *P. ponderosa* is accompanied by *P. Murrayana* (34 μ), which also has narrow spring tracheids. Again, according to MAYR, in a more northern Pacific region, where during the vegetative season the prevailing relative atmospheric humidity is 80–63 per cent, Douglas fir exists; but when the humidity sinks to 54 per cent, Douglas fir is replaced by *P. ponderosa*. MAYR ranges Pacific pines found growing in warm temperate regions as follows, according to their demands for moisture, beginning with those demanding most moisture:

Soil moisture: *P. Jeffreyi* (47 μ), *P. Lambertiana* (45 μ), *P. ponderosa* (29.5 μ), *P. Coulteri* (39.5 μ).

Atmospheric moisture: *P. Lambertiana* (45 μ), *P. Jeffreyi* (47 μ), *P. Coulteri* (39.5 μ), *P. ponderosa* (29.5 μ).

Thus, in these pines which replace one another from site to site, the two with widest spring tracheids demand more moisture than the other two. It is worthy of note that the moisture-loving haploxylic *P. Lambertiana* has narrower spring tracheids than the

TABLE II

PINUS, SECTION II

Letters indicating general distribution are as follows: A, Atlantic; P, Pacific; M, North Mexican.

	Mean diameter of spring tracheids			Distribution, soil, altitude, etc.
	Pseudo-strobus	Taeda	Pinaster	
1. P. ponderosa	....	29.5(P)	....	Dry rocky ridges, dry valleys, rarely in cold swamps; warm temperate; British Columbia to North Mexico (see subsequent comments).
2. P. tuberculata	....	30(P)	....	Dry sandy-gravelly slopes and ridges of Sierra Nevada and Coast Mts. from Oregon to California, 2500–5000 ft.; nearly subtropical.
3. P. rigida	....	33(A)	....	Dry gravelly uplands, sandy plains, cold deep swamps; Canada to N. Georgia; warm temperate; sometimes with *P. echinata*.
4. P. Murrayana	....	....	34(P)	Alaska to S. California and Arizona; on Sierra Nevada at 8000–9000 ft.; often on dry gravel; cool temperate.
5. P. muricata	....	....	35.5(P)	Cold peat bogs, barren sandy gravel, sea slopes of Coast Mts. of S. California; subtropical.
6. P. inops	....	....	36(A)	Sandy barren soil, dry heights; New York to South Carolina and Indiana; can be grown on the worst types of dry soil (dunes, etc.); warm temperate.
7. P. contorta	....	....	37(A)	Sphagnum bogs, sand dunes, exposed rocky sites, near the coast from Alaska to California; warm temperate.
8. P. arizonica	38(M)	....	....	Mountains of S. Arizona, Chihuahua, and Sonora; 6000–8000 ft.; warm temperate.
9. P. chihuahuana	....	38.5(M)	....	Mountains of New Mexico, Arizona, Chihuahua, and Sonora; 6000–7000 ft.; warm temperate to subtropical.
10. P. Torreyana	38.5(P)	....	....	On sand or sandy loam on the coast of California, where it is exposed to the wind, which often causes it to assume a partly prostrate habit; subtropical.
11. P. pungens	....	....	39(A)	Dry gravelly slopes of the Alleghany Mts. up to 3000 ft.; warm temperate.

TABLE II—*Continued*

	Mean diameter of spring tracheids			Distribution, soil, altitude, etc.
	Pseudo-strobus	Taeda	Pinaster	
12. P. Coulteri.....	....	39.5(P)	....	Warm dry slopes on the coast ranges of California; 3000–6000 ft.; warm temperate (see subsequent comments).
13. P. sabiniana....	....	39.5(P)	....	Dry foothills of W. California, among evergreen oaks; subtropical.
14. P. insignis.....	....	40(P)	....	Sandy soil on coast of California; subtropical (see subsequent comments).
15. P. Banksiana...	....	....	43(A)	Sandy soil to loam, capable of growing on very dry barren soil or even in peat bogs; Canada to Minnesota, etc.; cool temperate.
16. P. resinosa.....	....	....	44(A)	Sandy soil, usually in less dry soil than *P. Banksiana;* widespread in Canada and N.E. United States; warm temperate.
17. P. glabra*.....	....	....	(44) } 37(A) }	Moist sand or rather moist forest soil; South Carolina to Florida; subtropical.
18. P. cubensis.....	....	44(A)	....	Subtropical and tropical, on land just above flood area; South Carolina, Florida, West Indies, etc.
19. P. serotina.....	....	47(A)	....	"The pond pine," at margin of swamps in wetter soil than *P. cubensis;* N. Carolina to Florida; subtropical.
20. P. Jeffreyi.....	....	47(P)	....	Moist sandy gravel on mountains in California; 6000–8000 ft.; warm temperate (see subsequent comments).
21. P. clausa......	....	....	48(A)	Barren stretches of sand on higher ground than *P. cubensis;* Alabama to Florida, coast of Gulf of Mexico; subtropical.
22. P. echinata.....	....	....	48(A)	New York to Florida, Louisiana, and Texas; subtropical.
23. P. palustris.....	....	49(A)	....	Sand, often coarse, rarely low wet soil, never in swamps; along the coast from S.E. Virginia along the Gulf of Mexico to Mississippi.
24. P. Taeda......	....	49.5(A)	....	Low wet clay or sand, less dry and more loamy soil than *P. palustris;* S. Delaware to Florida, Texas, Arkansas, etc.
25. P. tropicalis†...	....	50.8(A)	50.8(A)	Tropical; Cuba, Isle of Pines.

* 44 is my own measurement; 37 that recorded by Penhallow.

† As to the synonymy, and consequently the section to which this pine belongs, I am not informed.

diploxylic *P. Jeffreyi* of apparently similar moisture-demanding habits. The other two with narrowest tracheids are both obviously xerophilous as regards edaphic conditions, and one of them is also climatically so in so far as it is a Pacific species.

As a second group of species may be taken those with narrow spring tracheids, between 34 and 37 μ in diameter. All these occupy physically or physiologically dry soils, or where the evidence of this is least obvious, as in *P. Murrayana*, the species often accompanies *P. ponderosa*. Although *P. inops* (36 μ) occasionally is distributed together with two species belonging to the moist subtropical Atlantic region, namely *P. echinata* (48 μ) and *P. Taeda* (49.5 μ), it is in areas less moist than that region, where *P. rigida* (33 μ) is also encountered.

The next two species, *P. arizonica* (38 μ) and *P. chihuahuana* (38.5 μ), mingling on the mountains of dry Mexico, agree closely in diameter of spring tracheids, although the two species belong to different systematic subdivision of section II of *Pinus*. Closely agreeing with them is *P. pungens* (38.5 μ), which belongs to the same systematic group as *P. arizonica* and is xerophilous in distribution on the Pacific Coast.

The fourth group containing four species, with width of spring tracheids between 39 and 40 μ, includes one Atlantic species growing in very pervious soil (gravel) and three Pacific species growing on soils that we may presume are not pervious gravels, for *P. Coulteri* grows on gravelly loam and *P. insignis* occupies sand and is used to fix sand dunes, being apparently uninjured by the salt water flung over its roots by spring tides (MAYR). Comparison between *P. Coulteri* and *P. ponderosa*, which endures greater drought, has been made above.

The next two species, with the width of spring tracheids between 43 and 44 μ, differ from all those previously discussed in being largely cool temperate in distribution; they are northern forms. So far as supply of moisture is concerned, it is difficult to see why the cool temperate *P. Banksiana* (43 μ) should have relatively wide tracheids, as it can grow well on dry barren sand or in peat bogs; and even *P. resinosa* (44 μ) for a time can endure dry sand. It may be that, just as with a higher temperature of climate, trees require a higher rainfall, so if narrowness of spring tracheids be a form of protection against desiccation, cold temperate pines might be able to afford to have wider tracheids than warm temperate growing in equally dry situations. *P. Banksiana* (43 μ) has narrower tracheids than *P. resinosa* (44 μ), which usually grows in less dry places. These two species are accompanied often by the haploxylic moisture-loving *P. Strobus* (41.5 μ), whose spring tracheids are narrower, just as is the case with the haploxylic *P. Lambertiana* compared with its diploxylic occasional companion, *P. Jeffreyi*.

The remaining species, excepting *P. Jeffreyi*, are subtropical Atlantic, occurring near the coast in a region where there is a heavy rainfall during summer and winter, and the air is moist. It is significant that in this group of pines possessing the widest spring tracheids, these latter agree sufficiently in diameter whether the species belong to the section TAEDA or to PINASTER. First, there are two, one belonging to each section, with a diameter of 44 μ; then there are four belonging to TAEDA, two with the diameter 47 μ, and two with 49 μ and 49.5 μ, respectively. Lastly, there are two belonging to PINASTER, with the diameter of 48 μ. The species that is the most clearly tropical in distribution is the one having the widest spring tracheids; and such is likewise the case in India where the tropical *P. Merkusii* grows on sites receiving, at least periodically, very considerable supplies of moisture.

If again we range the species in accordance with MAYR's grouping as subtropical, warm temperate, cool temperate, and alpine, in order so far as possible to determine temperature as a factor, the following facts come out.

Subtropical.—The five diploxylic species (nos. 2, 5, 10, 13, 14 in table II), characterized by narrow spring tracheids ranging from 30 to 40 μ, are all Pacific species, with or without marked perviousness of soil. The remaining diploxylic species (nos. 17, 18, 19, 21, 23, 24, 25), having wider spring tracheids, are Atlantic species living in a moist climate. The Pacific and Atlantic groups both include representatives of the sections TAEDA and PINASTER.

Warm temperate.—The first six diploxylic species, with the narrowest spring tracheids ranging from 29.5 to 38.5 μ, include two

Pacific species (nos. 1 and 7) and two Atlantic species (nos. 3 and 6), all four of xerophilous habitat; also two Mexican species (nos. 8 and 9) growing in a dry climate and at least sometimes on dry soil. The three species with widest spring tracheids include two Pacific species (nos. 16 and 20), definitely showing larger demands for moisture of soil and air than the other Pacific warm temperate species, and one Atlantic species (*P. resinosa*) that is not edaphically xerophilous as are the other Atlantic species in this warm temperate group. There is not the sharp contrast between the Pacific and Atlantic species that there is in the subtropical group, possibly because the Pacific species are not at so great a disadvantage as regards supplies of moisture, either because they belong to the northern Pacific, which is characteristically moister than the southern (no. 1 partly, and no. 7), or because they grow on mountains where the climate is moist (nos. 12 and 20), while the Atlantic species with warm tracheids are definitely in dry soils.

Cool temperate and alpine species.—Of the two diploxylic species ranged under this heading, *P. Murrayana*, the Pacific species often on dry ground and reaching alpine situations, has narrower spring tracheids (34 μ) than has the other, *P. Banksiana* (43 μ), though this latter can grow on very dry soils.

Summary.—The American species of *Pinus* having the narrowest spring tracheids are all more or less markedly xerophilous in distribution; those with the widest spring tracheids are all subtropical and more or less hygrophilous in distribution. The few East Indian species show similar characters in this respect. In section I of *Pinus*, so far as the measured American and East Indian species are concerned, differences in tracheid width run parallel with distinction in systematic affinity, thus suggesting that the evolution of the different groups of this section has been determined by the available water supply.

Other North American Coniferae

The succeeding table records the width of the spring tracheids as given by PENHALLOW, and the distribution of other American conifers.

Table III shows that evidence in favor of the view that scantiness and abundance of available water supply are respectively

TABLE III

	Width of spring tracheids in μ			Distribution, soil, altitude, etc.
	Atlantic	North Mexican	Pacific	
Torreya—				
T. californica	......	......	38	California, 3000–5000 ft., moist soil near streams; subtropical.
T. taxifolia	40	......	......	W. Florida, moist soil; moderately warm.
Sequoia—				
S. gigantea	......	......	39	Warm temperate.
S. sempervirens	......	......	55	Very moist soil and moist air; subtropical.
Chamaecyparis—				
C. Lawsoniana	......	......	18	S.W. Oregon and California, moist soil; warm temperate.
C. nutkaensis	......	......	25.5	Alaska to British Columbia, Cascade Mts.; adapted to the moistest air and a larger rainfall than *C. Lawsoniana;* warm to cool temperate.
C. thyoides	32	......	......	Maine to N. Florida; cold swamps.
Cupressus—				
C. arizonica	......	25	......	Arizona, Sonora, Chihuahua, 3000–5000 ft.
C. Macnabiana	......	......	30	California, dry hills and low slopes; subtropical.
C. Goveniana	......	......	32	California coast up to 3000 ft., hot rocky slopes, often on banks of streams; tropical.
C. macrocarpa	......	......	39	California, south of Monterey Bay, exposed constantly to the sea breezes; subtropical.
Juniperus—				
J. sabinoides	......	17	......	Texas to Mexico; up to the limits of vegetation on high mountains in Central Mexico.
J. nana	18	......	......	Labrador to New York and Utah.
J. californica	......	......	18	Sacramento River to Lower California; dry mountain slopes, desert slopes of Tehachapi Mts.; subtropical.
J. occidentalis	......	......	18	6000–10,000 ft., dry rocky ridges of Blue Mts., where it is a shrub on dry hot ridges; cool temperate.
J. monosperma	......	19	......	Rocky Mts. to Arizona and Mexico, 3500–7000 ft., gravelly slopes.
J. communis	......	......	20.5	Greenland to mountains of California and Arizona.
J. pachyphlaea	......	21	......	S.W. Texas to desert ranges of Arizona, 4000–6000 ft., arid mountain slopes; subtropical.
J. Sabina	21.5	......	......	Nova Scotia to Rocky Mts. and Montana; slopes and river banks.

TABLE III—*Continued*

	Width of spring tracheids in μ			Distribution, soil, altitude, etc.
	Atlantic	North Mexican	Pacific	
Juniperus (*cont.*)—				
J. utahensis	......	23	......	Rocky Mts. to Sierra Nevada, up to 8000 ft., arid hills and slopes.
J. virginiana	32	......	32	New Brunswick to Florida and tropical forests; Atlantic Coast to the prairies (100° W.) north of 54° N.; snowy summits of Rocky Mts., sea coast of British Columbia; rocky, dry, gravelly soil, sterile sand, meadow, moist, or swampy soil; cold to tropical.
Larix—				
L. americana	39.5	......	......	Arctic to West Virginia; in the north on well drained uplands, in the south in cold deep swamps; cool temperate.
L. occidentalis	......	......	42	British Columbia to Oregon, Montana, and Idaho, 2000–7000 ft.; moist bottom lands and dry mountain slopes; cool temperate.
L. Lyallii	......	......	43	Alberta and British Columbia, 7000–8000 ft. near timber line; "alpine."
Picea—				
P. rubra	29.5	......	......	Prince Edward Island to N. Carolina; well drained uplands and mountain slopes.
P. Breweriana	......	......	33	California and Oregon, 4000–7000 ft.; mountain peaks and ridges, near the timber line; "alpine."
P. alba	33.5	......	......	Labrador to New York to Montana; in the southern regions it is a low tree in swamps; it extends far north into permanently icy ground; cool temperate.
P. sitchensis	......	......	34	Alaska to California; moist sand or swamp, or wet rocky slopes in the north; solely coastal (within 50 miles of coast); more sensitive to dryness than to cold.
P. nigra	34.5	......	......	Alaska to Labrador to Virginia; in the north in well drained bottom lands; in the south in swamps and sphagnum bogs.
P. Engelmanni	......	......	35	British Columbia (5000 ft.), Arizona (11,500 ft.), high mountain slopes, well developed in moist canyons, very high up becomes shrubby; cool temperate.
P. pungens	......	......	38	Wyoming to Colorado and Utah, 6500–10,000 ft.; banks of streams, moist valleys; cool temperate.

TABLE III—*Continued*

	Width of spring tracheids in μ			Distribution, soil, altitude, etc.
	Atlantic	North Mexican	Pacific	
Abies—				
A. Fraseri	30.5	......	......	S.W. Virginia to Tennessee, 4000–6000 ft., on moist slopes.
A. lasiocarpa	......	......	33.5	Alaska to Arizona; 4000 ft. in British Columbia; 12,000 ft. in Colorado; "alpine."
A. magnifica	......	......	38.5	S. Oregon, 5000–7000 ft.; Sierra Nevada 6000–10,000 ft.; cool temperate.
A. concolor	......	......	39	S. Colorado to California and arid regions of New Mexico and Arizona; "moist canyons" of Californian Sierras; warm cool temperate.
A. amabilis	......	......	40	British Columbia to Oregon, high mountain slopes, often with *A. nobilis;* cool temperate.
A. balsamea	40	......	......	Labrador to mountains of S.W. Virginia; often in low swampy ground or on well drained soil, often with *Picea alba;* cool temperate.
A. nobilis	......	......	41	Cascade Mts., Washington to California, 2500–5000 ft., often with *A. amabilis;* warm to cool temperate.
A. bracteata	......	......	41.5	California, 3000–6000 ft., moist cool soil.
A. grandis	......	......	49.5	Vancouver to California, Idaho, Oregon, Montana; near the coast on moist ground; in the interior on moist slopes; 2500–7000 ft.; warm temperate.

associated with narrowness and wideness of spring tracheids in the different species or genera is provided by *Torreya*, *Chamaecyparis*, *Sequoia*, and *Juniperus;* somewhat favoring the view are *Cupressus* and *Picea;* indifferent in indication from this standpoint are *Abies* and *Larix.*

The enumerated species of *Juniperus* all seem to be actually or potentially xerophilous in habitat, and, with one exception, have very narrow spring tracheids (17–23 μ). The one exception is *J. virginiana*, which has rather narrow spring tracheids, and a remarkable range of distribution as regards climate and soil (it is possible that the specimen of wood measured was derived from a tree growing in a moist site).

Contrasting with *Juniperus* is *Torreya,* in which both species inhabit moist places and have relatively wide spring tracheids, 38 μ in the Pacific species, and 40 μ in *T. taxifolia* of the moister climate of Western Florida.

Sequoia sempervirens (55 μ), which not only has larger leaves but also grows in a warmer and damper climate and moister soil than *S. gigantea* (39 μ), exceeds all other measures of North American Coniferae in width of spring tracheids.

Of the two Pacific species of *Chamaecyparis*, *C. Lawsoniana* (18 μ) has unexpectedly narrow spring tracheids, for it grows preferably on moist soil. Compared with it, *C. nutkaensis* has wider spring tracheids (25.5 μ) and grows in cooler and much moister regions, where it is limited to places having the moistest of air. Still wider spring tracheids are those of the Atlantic *C. thyoides* (32 μ), though it grows in cold swamps.

Cupressus arizonica (25 μ), living in the driest region (Mexican), is likewise the species with narrowest spring tracheids. The three other species measured are Californian, and the one with narrowest spring tracheids, *C. Macnabiana* (30 μ), appears to be the one of the least moist habitat, for *C. Goveniana* (32 μ) is said to occur often on the banks of streams, while *C. macrocarpa* (39 μ) is constantly in damp sea air. Yet this last species can be used with *Pinus insignis* to fix sand dunes, and its roots can be laved with sea water, so that without further investigation it is impossible to say that *Cupressus*, as a whole, definitely favors the view here propounded.

The American species of *Abies*, whose tracheids have been measured, neither clearly support nor oppose the view. True it is that *A. lasiocarpa* (33.5 μ), the species that is nearly alpine and is described as "alpine," has with one exception the narrowest spring tracheids, but that exception is *A. Fraseri* (30.5 μ), which grows on moist slopes in moist cool air. So far as habitat is concerned, there appears to be no reason why *A. Fraseri* (30 μ) should have much narrower tracheids than the more northern Atlantic form *A. balsamea* (40 μ), which indeed often grows in swamps, and sometimes even sphagnum swamps, unless, indeed, the cause be the same as that already suggested in connection with the parallel cases of *Pinus Banksiana* and *P. resinosa;* apparently *A. balsamea* and *P. Banksiana* are found growing together.

Of the genus *Picea*, *P. rubra* (29.5 μ) is the species having the narrowest spring tracheids. Of the next two species, *P. Breweriana* (33 μ) is the only American Pacific alpine (or subalpine) species; while *P. alba* (33.5 μ) goes very far north, where, according to MAYR, it can grow on permanently icy soil. Farther south *P. alba* often occurs in swamps, including occasionally sphagnum bogs, and frequently mingles with *P. nigra* (34.5 μ). The remaining three species, *P. sitchensis* (34 μ), *P. Engelmanni* (35 μ), and *P. pungens* (38 μ), grow in places where air and soil are moist. Thus the three species whose habitats are regularly or potentially xerophilous have the narrow spring tracheids, whereas the two species with the widest spring tracheids show clear demands for more moisture. Yet this indication is weakened by *P. rubra* and *P. sitchensis*. The three Atlantic species (29.5–34.5 μ) belong to the section MORINDA; of the four Pacific species, *P. Breweriana* (33 μ) is in section OMORICA, while the other three (34–38 μ) belong to CASICTA, and their delicate loose cone scales seem to suggest that moistness of air characterizes their habitat.

Larix shows the narrowest spring tracheids in *L. americana* (39.5 μ), which reaches arctic sites, and, when farther south (reaching Virginia), grows in cold deep swamps, and particularly occurs in sphagnum swamps. Of the other two species, *L. occidentalis* (42 μ) and *L. Lyallii* (43 μ) differ but little in width of spring tracheids, but the one with wider tracheids is that which is nearly alpine, in fact is often termed "alpine." Thus *Larix* gives no clear indication of a correlation between narrowness of tracheid and xerophily of habitat. Compared with the evergreen conifers of the same habitat, the spring tracheids of *Larix* are usually wider, as might be anticipated (1).

In connection with the question of the influence of two of the factors deciding the width of the spring tracheids, namely systematic affinity and habitat, some suggestive results are yielded by a comparison of these widths in different species occupying the same habitats.

In the northern Atlantic region, *Abies Fraseri* (30.5 μ) and *Picea nigra* (34.5 μ) often grow together, as do *Abies balsamea* (40 μ) and *Picea alba* (33.5 μ). These two species of *Picea*, only slightly differing in tracheid width, often mingle; thus in a second manner is shown that there is some problem as to the unexpected width of spring tracheids in *Abies balsamea*. *Juniperus virginiana* (32 μ) often mingles with the two species of *Picea* in moist ground and does not differ much from them in tracheid width. But *Pinus Strobus* (41.5 μ), often replacing these three species, and *Pinus Banksiana* (43 μ), often occurring with *Picea alba*, though agreeing fairly with one another, have much wider tracheids than these three species. *Larix americana* (39.5 μ) often largely replaces *Abies balsamea* (40 μ) and *Picea alba* (33.5 μ) on sphagnum bogs.

On the warm temperate Pacific coast, *Pinus insignis* (40 μ) and *Cupressus macrocarpa* (39 μ) are often grown together as dune fixers, and nearly agree in tracheid width.

Still closer agreement characterizes *Abies concolor* (39 μ) and *Sequoia gigantea* (39 μ), which are often associated in the warm to cool temperate Pacific forests. Again, the equivalent species of *Pinus* have relatively wide spring tracheids, for *P. Jeffreyi* (47 μ) often is associated with *Abies concolor* (39 μ), whose demands for moisture are about equal to those of *P. Lambertiana* (45 μ) (MAYR).

In the cool temperate Pacific region, the deciduous *Larix occidentalis* (42 μ) has much wider spring tracheids than its frequent companion *Pinus Murrayana* (34 μ); while *Abies nobilis* (41 μ) and *Abies amabilis* (40 μ), which occur together, differ only slightly in width of spring tracheids.

In the Pacific so-called alpine region, there is a remarkable approximate agreement in the width of spring tracheids in three genera: *Abies lasiocarpa* (33.5 μ), *Picea Breweriana* (33 μ), *Pinus Balfouriana* (32 μ), *Pinus aristata* (33.5 μ), and *Pinus albicaulis* (35 μ). All these contrast with the alpine larch, *Larix Lyallii* (43 μ), whose wide tracheids correspond with the deciduous habit.

American deciduous species of Quercus

In a previous paper (1) I have shown that the width of the spring vessels in *Quercus* is decided partly by the habit of the species, and that these vessels are wider in deciduous than in evergreen species, even though the latter may grow in moist Florida, as is the case with *Q. virginiana*. The subjoined statistics suggest strongly

TABLE IV

AMERICAN DECIDUOUS SPECIES OF QUERCUS

W, white oaks; B, black oaks; all are warm temperate excepting *Q. lobata*, which is subtropical.

	Width of widest spring vessels				Habitat
	Atlantic		Pacific		
	W	B	W	B	
Q. Garryana	......	......	0.338	......	Dry habitat; Vancouver to California and Oregon; dry gravelly slopes of low hills; also between prairie and pine forests.
Q. lobata	......	......	0.356	......	Subtropical (in the same region as the evergreen *Q. chrysolepis*, *Q. Wislizeni*, and *Q. agrifolia*) in California; often after losing its leaves in dry autumn, acquires fresh ones after rain in November, hence tending to be sub-evergreen.
Q. obtusiloba	0.362	......	......	......	Dry sandy gravel, or on hard impervious loam where dryness and moistness alternate suddenly; Cape Cod to Florida, Mississippi, Texas, etc.
Q. macrocarpa	0.372	......	......	......	Variable as regards soil, but showing power of enduring some degree of dryness by growing on higher sites at the edge of prairie or on dry hills in northwest region of its area, which is wide, extending from Nova Scotia and Ontario to Minnesota, Texas, etc.
Q. Macdonaldi	......	......	0.372	......	Islands off California.
Q. californica	......	......	......	0.378	W. Oregon, coast ranges of California, 7000–8000 ft. in western slopes of Cascade Mts., to mountains of S. California (optimum 6000 ft.).
Q. Prinus	0.387	......	......	......	Various habitats; Ontario to Alabama, Tennessee, etc.
Q. rubra	......	0.387	......	......	No special soil; goes farther north than any other American oak, and on Alleghany Mts. ascends into the fir region.
Q. coccinea	......	0.412	......	......	Usually light sand, but also dry gravelly uplands and prairies; Ontario to Alleghany Mts., and North Carolina to Nebraska, etc.
Q. tinctoria	......	0.412	......	......	Dry gravelly uplands and ridges; Ontario to Minnesota, Florida, Mississippi, Texas, etc.
Q. palustris	......	0.419	......	......	Good wet soil (not swamp) at the edges of swamps and margins of rivers; Canada to Missouri, Virginia, Arkansas, etc.

TABLE IV—*Continued*

	Width of widest spring vessels				Habitat
	Atlantic		Pacific		
	W	B	W	B	
Q. aquatica	......	0.438	......	......	Sandy borders of swamps; Delaware to Florida, Gulf States, Texas, Oklahoma, etc.
Q. Muhlenbergii	0.444	......	......	......	Variable habitat; dry hills to deep rich bottom lands and rocky banks of streams; Ontario to Columbia, N. Louisiana, Texas, etc.
Q. alba	0.45	......	......	......	Optimum soil is fresh (rather moist) loam in undulating country or on the banks of streams; but the habitat varies from sandy plains to gravelly ridges; Ontario to N. Florida, Minnesota, Texas, etc.
Q. bicolor	0.45	......	......	......	Borders of streams and swamps; Ontario to N. Georgia and W. Missouri; does not extend so far south as *Q. alba*.
Q. Michauxii	0.587	......	......	......	Borders of swamps and streams; Delaware to Florida, Gulf States, Kentucky, etc.

that in the deciduous species width of spring vessel is at least largely determined by systematic affinity and by available water supply; the spring vessels being narrower in species belonging to physically or physiologically drier places, and for the same type of habitat being narrower in black oaks than in white oaks.

The points of significance in connection with the deciduous oaks are:

1. Of the six species with narrowest spring vessels (0.338–0.378 μ), four are Pacific species and characterized by drier climate than the Atlantic species. Among the four Pacific species, the one with the narrowest vessels is the one whose soil is definitely stated to be dry gravel. The second is subtropical in the region of evergreen species, and itself approaches the evergreen stage. Of the other two, one has a maritime climate, and the other no dryness of habitat (apart from the Pacific climate). Of the two Atlantic species, one occupies an edaphically dry habitat, while the other, though variable as regards habitat, shows a power of living on at least rather dry sites.

2. Considering the Atlantic species, and taking separately the two series representing respectively the white oaks and black oaks, the former of these begins with the two species just referred to, continues with two species of variable habitat as regards soil, passes to one in which the optimum soil is rather moist but varies, and concludes with two species confined to thoroughly moist soil. The last of these also occurs in the region where the American pines exhibit the greatest caliber of tracheids, namely, Florida and the Gulf States.

The series of Atlantic black oaks commences with wider vessels than the series of white oaks. The first species shows no special choice of soil, but can grow farther north than any other American warm temperate species; the next two species clearly show preference for dry situations, or at least a capacity for thriving on dry gravels; the series, like that of the Atlantic white oaks, concludes with two species confined to thoroughly moist soil on the borders of swamps and rivers.

Summary

1. There is considerable evidence that the width of the spring tracheids in evergreen Coniferae is largely decided by two factors, systematic affinity and available water supply. So far as the latter is concerned, the spring tracheids are generally narrowest in species of xerophilous habitat.

2. In American species of *Pinus* belonging to section I (Haploxylon), variation in the width of the spring tracheids runs quite parallel with difference of systematic affinity and of available water supply (including influences promoting transpiration). Thus the first step in the evolution of this section of *Pinus* would appear to have been a division into a more xerophilous type (ancestral PARACEMBRA), and a less xerophilous type (ancestral CEMBRA), and each of these subsections would appear to have undergone similar division into more or less xerophilous groups, that is, into PARRYA and BALFOURIA, also EU-CEMBRA and STROBUS. The two East Indian species, *P. Gerardiana* and *P. excelsa*, structurally accord with this theory.

3. Among American species of *Pinus* belonging to section II (Diploxylon), those with narrow spring tracheids are more xerophi-

lous in distribution, while those with the widest tracheids belong to a subtropical or tropical moist climate. Though in general this section of *Pinus* supports the theory given in paragraph 1, there are in it certain species in which width of tracheid does not appear to correspond with the supply of available water. Such discrepancies, whether real or only apparent, may be due to one or more of the intervening causes mentioned in paragraph 6.

4. Species of other North American genera of evergreen Coniferae show differences in the width of spring tracheids that may possibly be partly due to differences in affinity; as species of the same habitat, but belonging to different genera, may differ considerably in tracheid width, or, on the other hand, may approximate to agreement. Some of these genera, namely, *Torreya*, *Chamaecyparis*, *Sequoia*, and *Juniperus*, support the view that the width of the spring tracheid is correlated with available water supply; somewhat favoring the view are *Cupressus* and *Picea;* indifferent in indication are *Abies* and *Larix*.

5. The theory here propounded derives support from measurements of the width of the spring vessels of American deciduous species of *Quercus*. For narrowness and wideness of spring vessels in the main are respectively associated with scantiness and abundance of water supply. But in the same kind of habitat the deciduous black oaks would seem to have narrower spring vessels than are possessed by the deciduous white oaks.

6. Though the evidence as a whole strongly favors the theory here propounded, much fuller information is necessary before a safe conclusion may be drawn. Hence this inquiry and the suggestions here given must be regarded as tentative and issued in the hope of stimulating inquiry in regard to factors that may intervene, such for instance as the following: climate (including evaporation power), exact soil water-content, level of water-table, etc., that form the environment of the different species of conifers; also, depth of root, duration of foliage and size of aggregate leaf surface, rate of transpiration, width of sap wood, etc., in the different species; also, variations within one and the same species in regard to the features just mentioned, as well as in the width of the spring tracheids, in different habitats.

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